

## BOOK REVIEWS

**The Nesting Behavior of Dung Beetles (Scarabaeinae). An Ecological and Evolutionary Approach.**—Gonzalo Halffter and W. D. Edmonds. 1982. Publication 10, Instituto de Ecologia, Mexico, D.F., 176 pp. \$40.00 in the United States and Canada, \$45.00 elsewhere. Available in North America from Bioquip Products, P.O. Box 61, Santa Monica, CA 90406.

Evolutionary? When I first saw the title of this book, I feared that it might simply be a clone of *The Natural History of Dung Beetles of the Subfamily Scarabaeinae (Coleoptera, Scarabaeidae)* by Halffter and Matthews (1966). While the lines of descent between these two works are clearly indicated, I was pleasantly surprised to see that the new book is not a rehash of old material at the expense of the reader's time and patience, but a delightful refinement and reanalysis of both old and new data on the nesting behavior of scarabaeines. The book is, appropriately enough, dedicated to Jean Henri Fabre, the French entomologist who first described in any detail the nesting behavior of dung beetles and who can be rightly considered the founder of dung beetle ethology. The contents of this current work add substantially to the cornerstone molded by Fabre in *Souvenirs Entomologique*. Halffter and Edmonds are both eminently qualified to address the nesting behavior of dung beetles because of their long and productive research with these animals.

The chapters are entitled (1) The Scarabaeinae, (2) The Ecological Evolution of Scarabaeinae, (3) Patterns of Nesting Behavior in Scarabaeinae: An Overview, (4) Evolution of Nesting Behavior and Sexual Cooperation, (5) Nest Construction and Architecture in Burrowing Scarabaeinae, (6) Other Sexual Relationships in Scarabaeinae, and (7) The Ovary and Nesting Behavior. The appendices are (1) Outline/Classification of the Subfamily Scarabaeinae, (2) Nidification Behavior of Old World Oniticellini by Yves Cambefort, (3) Nesting Strategies of Three Species of Coprophagous Scarabaeinae in the Sahel Region of Niger by Daniel and Christiane Rougon, and (4) Commentaries on Recent Literature. An extensive bibliography concludes the volume.

Chapter one is a general introduction to the subfamily Scarabaeinae and provides a good, concise picture of dung beetles. Also included is a very informative table comparing characteristics of scarabaeines, geotrupines and aphodiines. The major adaptive features of scarabaeines are listed as (1) food relocation behavior, (2) accentuation of body structure to enhance fossorial capabilities, (3) subterranean nesting behavior, (4) de-emphasis of courtship behavior, (5) increased male/female cooperation, (6) reduction in fecundity, (7) adaptation by larvae and pupae for development within an enclosed space, (8) mouthparts modified for soft food, and (9) adult digestive

tract modified to rapidly process large amounts of food. Halffter and Edmonds state that there is little doubt that the Scarabaeinae is a monophyletic group. I know of no substantive discussion concerning the derivation and/or presumed phylogeny of this group of scarabs, and such a *prima facie* statement seems out of place without further scientific evidence or documentation. With the vast array of morphological and behavioral data available to them, Halffter and Edmonds seem to be in an ideal position to now address such a phylogenetic analysis at the generic level, and we may hope that they will engage in such a project in the future.

The principal (and only) shortcoming in the first chapter is near the end of the third paragraph where the authors confuse the concepts of primitive and derived conditions in their discussion. Firstly, they indicate that “. . . coprophagy is the *primitive* (plesiomorphic) condition . . . and that it *derived from the general saprophagous habit* of the family; all other feeding behaviors (necrophagy, mycetophagy, *saprophagy*, etc.) we consider derived (apomorphic)” (italics mine). Their contention that coprophagy is *primitive* after having been *derived from* another state as well as calling saprophagy both primitive and derived in the same sentence are *non sequiturs*. Secondly, they use the terms *plesiomorphic* and *apomorphic* (indicating body structure) when they mean to use the terms *plesiotypic* or *apotypic* (referring to characters other than structure, such as behavior). It seems the authors attempted to use some catch words currently popular in the phylogenetics and evolution literature but tripped over their application. While initially confusing and somewhat bothersome, their foray into *terra incognita* should not detract from the overall value of the chapter.

Chapter two delves into the ecological evolution of dung beetles. The major adaptive features of the subfamily listed in chapter one are discussed in more detail using the framework of r- and K-selection theory to explain much of the exploitation of the soil/excrement system. The authors are quick to note that r- and K-selection represent extremes of a continuum, and that the evolution of any given species may result in a mixture of r- and K-selected traits; therefore, these concepts are relative. They conclude that the Scarabaeinae, relative to other scarabs and most other beetles, are essentially K-strategists. A convincing discussion follows of scarabaeine traits that exemplify the tactics assumed to be promoted by K-selection. These life history traits characteristic of Scarabaeinae are (1) survivorship influenced primarily by density dependent factors mostly operating directly on the adults, (2) ecological specialists, (3) delayed reproduction, slow development and repeated reproductive periods, (4) low fecundity and production of few, large sized offspring, (5) some degree of brood care, (6) low rates of juvenile mortality relative to adult mortality, and (7) superior competitors relative to other groups. This group of traits is a correlated set of adaptations which collectively define scarabaeines as K-strategists and as insects for which

ecological and reproductive efficiency is maximized. Prior to their discussion of evolutionary trends within the Scarabaeinae, the authors offer an *aplogia* for their lack of a statistically rigorous analysis of populations upon which to base largely quantitative theory. Their approach is that of natural historians and not population ecologists. No such apology is necessary for this method of establishing a working hypothesis. As the authors themselves point out, their experience has produced information that shows strong tendencies of consistency which demand explanation. Moreover (and much to their credit) Halffter and Edmonds distill all the descriptive data written on dung beetles and their own extensive observations into a persuasive, unified theory describing the ecological evolution of these animals, and they do this well. This chapter is the the most interesting and significant part of the book to me. It would be of supreme interest to see how the results of a study on the taxonomic evolution of these beetles would correlate with the scenario of behavioral evolution so expertly proposed by Halffter and Edmonds.

Chapter three explores the different ways dung beetles nest. A classification of nesting behaviors is included and is an extension and elaboration of that of Halffter and Matthews (1966) and Halffter (1977). A classification of nest morphologies, or patterns, is also provided. There is a great deal of descriptive information in this chapter which, although synoptic in nature, is valuable to understanding scarabaeine nidification behavior. It is here that we find much of the supportive evidence for the conclusions about ecological evolution proposed in the preceding chapter.

The fourth chapter explores the evolution of nesting behavior and sexual cooperation and, like chapter three, provides data supporting the conclusions reached in chapter two. Halffter and Edmonds conclude that nesting behaviors originated as derivatives of feeding behavior. Detailed discussion is given to the evolution of nesting behavior in burrowing scarabaeines and ball rolling scarabaeines respectively.

The next three chapters are largely descriptive. A detailed review of each nest type, the taxa constructing it, and the behavior associated with these taxa constitutes chapter five. The sixth chapter deals with sexual relationships with a summary of encounter and recognition, copulatory, and combat behaviors as well as bisexual cooperation independent of nesting. The last chapter relates the ovary of dung beetles to nesting behavior with the observation that there is a reduction in the number of maturing egg follicles as nesting behavior becomes more highly developed, i.e., there is greater parental care for fewer offspring.

The first appendix is an outline classification of the subfamily at the generic level. The classification differs in various respects to that given in Halffter and Matthews (1966). Immediately noticeable in this respect is the increased use of subgenera, a move that will be variably accepted depending, in large

measure, upon which side of the Atlantic a scarab systematist works. *Neocanthidium* continues as a valid genus even though it was synonymized by Howden and Young (1981); a difference of opinion, no doubt.

The papers by Cambefort and Rougon and Rougon constitute the next two appendices and result from a symposium held on evolution and nesting behavior in beetles. Cambefort details nicely the nesting behavior of Old World Oniticellini and formulates an evolutionary scenario for nest building in these insects. His first conclusion equates low fecundity with a primitive state which seems to be just the opposite conclusion reached by Halffter and Edmonds. Cambefort notes that additional species of Oniticellini must be studied before a firm idea of their behavioral and phylogenetic relationships can emerge.

The following short paper by the Rougons is a well executed descriptive work describing the nesting strategies of three African species that live in a very hot, dry climate.

The book is nicely produced on good quality paper. However, I found many of the photographs to be unclear because too coarse a photographic screen was used (see especially Fig. 65) and because of lack of suitable contrast. The line drawings are good, but many should have been reduced in size to eliminate their coarse look and provide snap to the illustrations. The size of the book (about 25 × 25 cm) is awkward because it will not conveniently rest on most book shelves without protruding excessively from the shelf. Editing is generally good although there are some glaring exceptions in the two invited papers and on p. 58 where there are six misspellings. Considering its moderate size, I thought the book was somewhat overpriced at \$40.00, but this seems to be a contagious malaise within the entire publishing industry.

In summary, then, I can strongly recommend this book. It will have its greatest appeal to scarab workers, coleopterists in general, ecologists, and those conducting research on the evolution of taxa, behavior, or ecological relationships. I know that some paleontologists as well as some applied entomologists have also been stimulated by this book. It will have broad appeal and application to anyone whose life is touched by these remarkable creatures.—*Brett C. Ratcliffe, Systematics Research Collections, W436 Nebraska Hall, University of Nebraska, Lincoln, Nebraska 68588-0514.*

#### LITERATURE CITED

- Fabre, J. H. 1920–1924. *Souvenirs Entomologique*. Librairie Delagrave, Paris, 383 pp. (English translation available.)
- Halffter, G. 1977. Evolution of nidification in the Scarabaeinae. *Quaest. Ent.* 13:231–253.
- Halffter, G. and E. G. Matthews. 1966. The Natural History of Dung Beetles of the Subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Fol. Ent. Mexicana* No. 12:1–312.
- Howden, H. F. and O. P. Young. 1981. Panamanian Scarabaeinae: taxonomy, distribution, and habits (Coleoptera, Scarabaeidae). *Contr. American Ent. Instit.* 18:1–204.